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Morphological study of the lingual papillae of the giant panda (*Ailuropoda melanoleuca*) by scanning electron microscopy

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Abstract

Due to the scarcity of giant pandas, there are few descriptions of their morphology and even fewer of their microscopic anatomy and the ultrastructure of their organs. In this study of the complete tongue of an adult male giant panda, we describe the morphology of its lingual surface, the different types of papillae, their characteristics and topographic distribution. It was seen that there are four main types of lingual papillae: filiform, conical, fungiform and vallate. There was no sign of foliate papillae, *tuberculum intermolare* or *sublingua*. Papilla distribution was not limited to the dorsum of the tongue, but was also seen on the anterior and ventral surfaces of the tongue. In the anterior third of the midline there is a smooth area with no papillae at all. Morphology of the microgrooves and pores is similar to that observed in other mammals. The papillae share characteristics encountered in Carnivora and herbivorous species of mammals. A narrow bamboo-based diet and specialized manner of eating have together resulted in modification of the tongue of a carnivoran, giving it some characteristics typical of an herbivore.
Key words giant panda; lingual papillae; scanning electron microscope; tongue.

Introduction

The giant panda has caused a great deal of controversy amongst zoologists with regard to its taxonomy. Since the first scientific descriptions by Armand David (David, 1869), the giant panda has been variously classified as a member of the Ursidae (bears) or Procyonidae (raccoons and their relatives), and has even been assigned to its very own family, Ailuropodidae (Thenius, 1979). Currently, thanks to genetic studies (O'Brien et al. 1985; Eichelberger et al. 1985; Goldman et al. 1989), it is recognized that it has closer associations with bears than with raccoons, although its divergence from other bears (Ursinae) goes back some 12 million years (Waits et al. 1999). The giant panda (*Ailuropoda melanoleuca*) is now included in the Ailurinae subfamily, within the Ursidae (Wilson & Reeder, 1993).

The varied morphologies of the tongues of vertebrates are generally the result of different strategies for capturing and manipulating food, grooming or vocal modulation. The lingual papillae contribute to some of these functions and, in addition, they accommodate the sense of taste, as is the case of the fungiform and vallate papillae. It is possible to speak of two types of papillae, mechanical and gustatory. The former perform the functions of trapping and creating a frictional surface for food and are an important element for grooming functions. The latter are those which contain the taste pores which lead to the sensory organs of taste, the taste buds.

The distribution of the different papillae on the surface of the tongue is characteristic of a genus and may even be distinctive for one species with regard to another. One of the elements that contributes most to the morphology, distribution and type of papillae is diet. The giant panda is the only carnivoran with an exclusively herbivorous diet based on up to 50 different species of bamboo shoots (Dierenfeld et al. 1982), which has caused its masticatory and especially, its digestive system (Sicher, 1944) to have been modified for this diet. It is an herbivorous carnivoran that has modified its ancestral morphology to accommodate its derived diet.

Early studies on the morphology of the surface of the tongue included those of Mayer (1844), Münch (1896) and later Sonntag (1923) (reviewed by Stadtmüller, 1938), who described the shape, situation and types of lingual papillae in different groups of mammals including species of the order Carnivora. In later years, various authors studied the morphology of the lingual surface in carnivorans with the scanning electron microscope (SEM) (Shimoda et al. 1996; Chamorro et al. 1987; Iwasaki et al. 1987a; Kobayashi et al. 1988; Emura et al. 2000a,b, 2004). In the case of Ursidae, amongst the few studies that have been made, those worthy of note include those of Inatomi & Kobayashi (1999),

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Table 1 Characteristics of giant pandas, with description of their tongues, in the literature

	Raven (1936)	Davis (1964)	Pastor et al. (2008)
Sex	Female	Male	Male
Age	(Adult)	1 years 4 months (estimated)	13 years 8 months
(Body)			
Weight	–	59.8 kg	102 kg
Snout to tail tip	146 cm	142 cm	–
(Tongue)			
Length	140 mm (incomplete)	210 mm	220 mm
Width	50 mm	55 mm	57 mm
Free portion	70 mm	75 mm	77 mm

in which they compared the tongues of the Japanese black bear (*Selenarctos thibetanus japonicus*) and the mountain goat (*Oreamnos americanus*), and Emura et al. (2001), dealing with the lingual surfaces of newborn Asian black bears (*Senelarctos thibetanus*) and leopard (*Panthera pardus*).

There have been several macroscopic descriptions of the tongue of the giant panda (Raven, 1936; Davis, 1964), but as yet no observation of the lingual surface has been undertaken with a scanning electron microscope (SEM).

The fact that this is an animal with a carnivoran's craniofacial structure and that it has adapted to an exclusively herbivorous diet with modified teeth (Davis, 1964) suggests that the tongue might also exhibit modifications related to its specialized diet. In the giant panda, as in primates, some other carnivorans and rodents, the tongue has lost its importance in the function of food prehension, since these animals use their paws to bring food to the mouth (Iwasaki, 2002). A better knowledge of the tongue in this rare animal may help us to improve our understanding of one of the most peculiar models of dietary adaptation known.

Materials and methods

We used a complete tongue of a male giant panda (*A. melanoleuca*), aged 13 years and 8 months, which had died of natural causes in the Zoo-Aquarium in Madrid. The weight of the specimen was 102 kg. Following extraction, the tongue was fixed by immersion in 10% formalin. Prior to visualization in the SEM, samples were taken of the lingual surface in different areas and post-fixed in a 1% solution of osmium tetroxide in a phosphate buffer for 4 h at room temperature. Subsequently, these were immersed in a solution of 8 N hydrochloric acid at room temperature for 15 min, to eliminate the remains of mucus and scaly cells (Evan et al. 1976). The samples were then washed in abundant water and dehydrated with increasingly graduated ethanols until reaching 100°. Following their dehydration, tissues were freeze-dried in a hyperbaric chamber (Balzers) of CO_2 and coated with gold in an argon (18 mV) vacuum chamber for 3 min. They were observed with a JEOL T-300 SEM with a 15 kV acceleration voltage. The samples have the corresponding CITES documentation.

Results

As in most carnivorans, the tongue of the adult giant panda is elongated with a rounded tip and smooth borders. The length from the tip to the glosso-epiglottic fold is 22 cm, with a maximum width of 5.7 cm, corresponding to the union of the middle third with the posterior third. The length of the free portion is 77 mm (Table 1). No pigmented area was observed and there was no evidence of an intermolar prominence, marginal folds or *sublingua*. In the middle region of the anterior third of the lingual dorsum, we observed a bare area devoid of papillae crossed by a longitudinal groove. The lingual papillae did not appear solely on the dorsum, but were observed also in the anterior ventral region.

Four types of papillae were clearly identified: conical, filiform, fungiform and vallate.

Conical papillae

These papillae appear on the posterior part of the dorsum, behind the vallate papillae. They are flattened in a craniocaudal direction and their lateral borders appear dentate with pseudo-papillary formations (Fig. 1). They are 1.8–3.4 mm in length and 0.5–0.8 mm in width at the base. Their surfaces are covered by microgrooves and pores can be observed (Fig. 2).

Filiform papillae

These are found on the whole of the dorsum. Two types can be clearly differentiated: multi-filamentous and crowned.

The multi-filamentous papillae are located on the dorsum of almost the entire surface of the tongue and in the anterior ventral region. The papillae on the dorsum are distributed from the tip to the margin of the vallate papillae, with the ends directed caudally. These papillae comprise a central papillary body from which emerge a variable number (from 3 to 12) of filiform projections, which are oriented in the same direction as the central papillary body (Fig. 3). Increased magnification reveals surfaces covered with microgrooves and pores (Fig. 4). The

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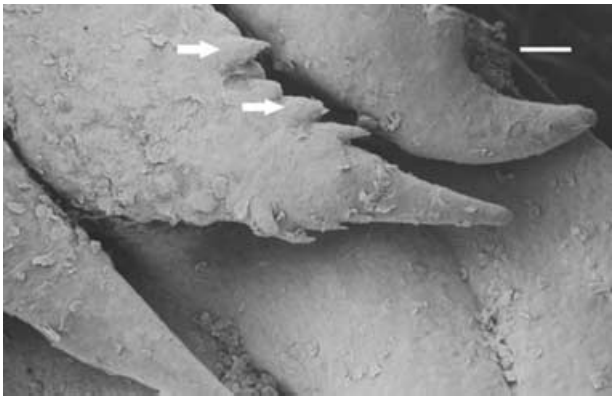

Fig. 1 Conical papillae situated behind the vallate papillae. (Arrows: pseudo-papillary formations on the edges.) 50×. Bar, 200 μm.

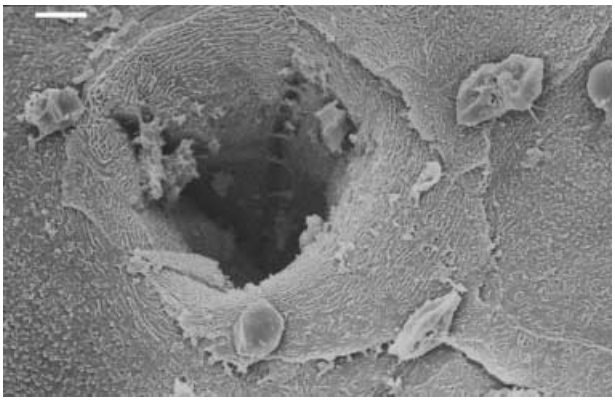

Fig. 2 Pore in a conical papilla situated behind the vallate papillae. 2000×. Bar, 5 μm.

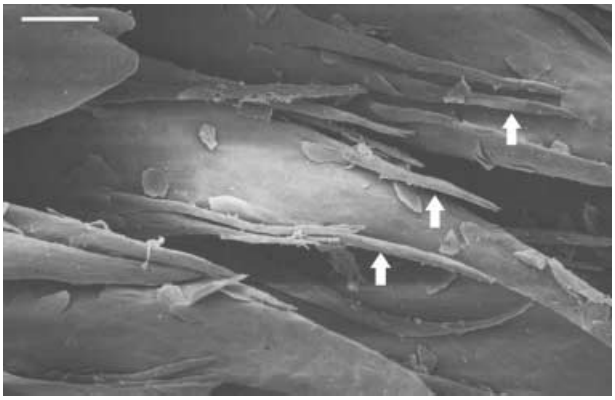

Fig. 3 Multi-filamentous filiform papillae situated on the tip of the tongue. (Arrows: Pseudo-papillary formations.) 150×. Bar, 100 μm.

multi-filamentous papillae of the ventral surface are larger than those of the dorsum, yet fewer in number. These have a base from which smaller pseudo-papillae extend. From the surface of the central papillary body and pseudo-papillae also emerge delicate projections which adhere to the central papilla, lying in the same direction. The orientation these papillae take is not uniform and they may be directed toward one another. Their length varies from 0.5 to 1.3 mm (Fig. 5).

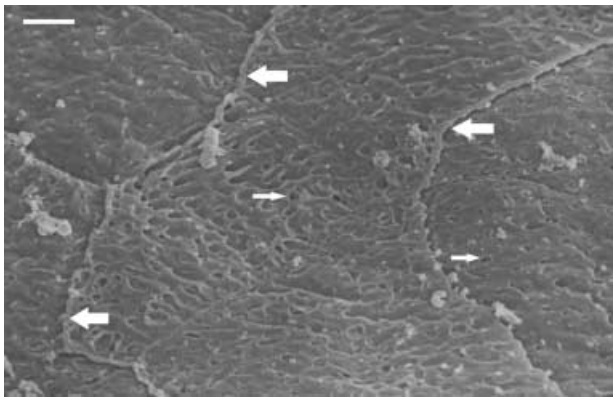

Fig. 4 Pores and cell unions on the surface of a multi-filamentous filiform papilla on the tip of the tongue. (Small arrows: pores; large arrows: cellular union.) 5000×. Bar, 2 μm.

Fig. 5 Multi-filamentous filiform papillae situated on the ventral surface of the tongue. (Arrows: pseudo-papillary formations.) 50×. Bar, 200 μm.

The crowned filiform papillae appear exclusively in the lateral regions of the anterior third of the tongue. Their base is circular, approximately 0.6–0.8 mm in width, and the two to eight projections which give them the form of a crown. These projections lie on the lateral margins of the papillae (Fig. 6).

Fungiform papillae

These are distributed along the entire dorsal surface, particularly on the anterior two thirds. Their size diminishes toward the tip of the tongue, ranging from 0.8 to 1 mm in diameter. Their morphology is typical one of fungiform papillae in other mammalian species: rounded and slightly convex (Fig. 7). On the entire perimeter they are surrounded, probably as a means of protection, by filiform

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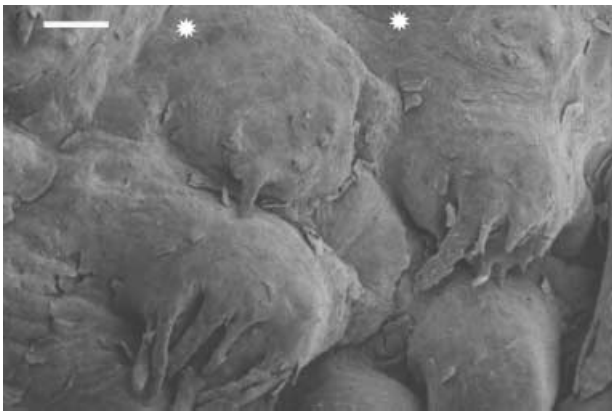

Fig. 6 Filiform papillae in a crown formation situated at the margins of the bare region. (*Bare region.) 50×. Bar, 200 μm.

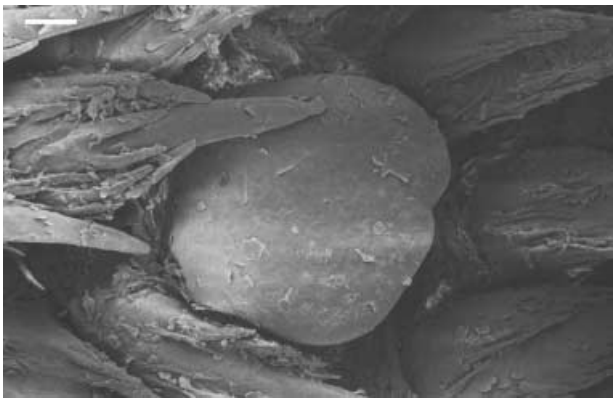

Fig. 7 Fungiform papilla surrounded by filiform papillae in the middle region of the tongue. 50×. Bar, 200 μm.

papillae. At greater magnification we can observe microgrooves and pores.

Vallate papillae

These are arranged in a V-pattern on the posterior third of the tongue with the apex of the V pointed anteriorly. In this particular specimen there are 11 vallate papillae, appearing either alone or forming pairs of smaller papillae. They are encircled by a deep, irregular groove within a poorly defined external disc with pseudo-papillary formations. The body of the papilla is rounded and made up of multiple secondary papillae separated by secondary grooves varying in depth (Fig. 8). Papillary size ranges from 1.5 to 3 mm in diameter. At greater magnification, multiple microgrooves and pores are evident (Fig. 9). Finally, on the anterior third of the tongue's surface there is a smooth area devoid of papillae with a well-defined groove running anteroposteriorly. In the margins of this area are situated the crowned filiform papillae (Fig. 10), and at increased magnification a mass of well-defined microgrooves can be observed (Fig. 11).

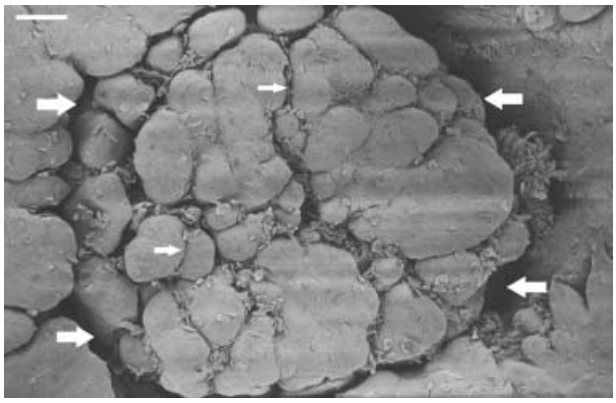

Fig. 8 Vallate papilla surrounded by a primary groove (large arrows) and multiple secondary grooves (small arrows) in the interior. 50×. Bar, 200 μm.

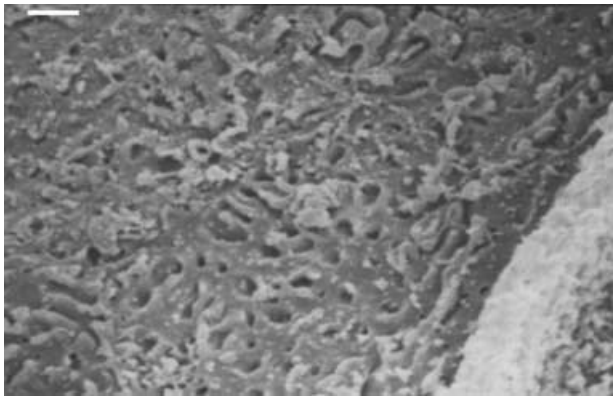

Fig. 9 Pores on the surface of the body of a vallate papilla. 10 000×. Bar, 1 μm.

Discussion

The technique employing hydrochloric acid to eliminate mucus and scaly cells, proposed by Evans et al. (1976), was effective although it was not possible to clean the tongue perfectly due to the formalin fixation.

Despite the similarity in the descriptions given by Raven (1936) and Davis (1964), those of Davis are more detailed, owing to the fact that the tongue he used was complete, and extraction and preservation were carried out in a laboratory. The dimensions of our specimen are close to those reported by Davis (1964) (Table 1).

Morphology and distribution of the papillae

Conical papillae

These are included by various authors in the group of filiform papillae (Barone, 1976; Scala et al. 1993; Shimoda, 1996; Emura et al. 2000c), although in this case, along with Sonntag (1920), Chamorro et al. (1987), De Paz et al.

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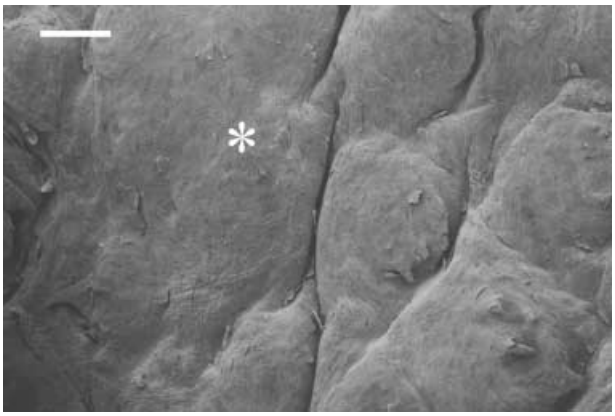

Fig. 10 Bare region in the central part of the lingual third anterior. Crowned filiform papillae appear externally. (*Linea media.) 50×. Bar, 200 μm.

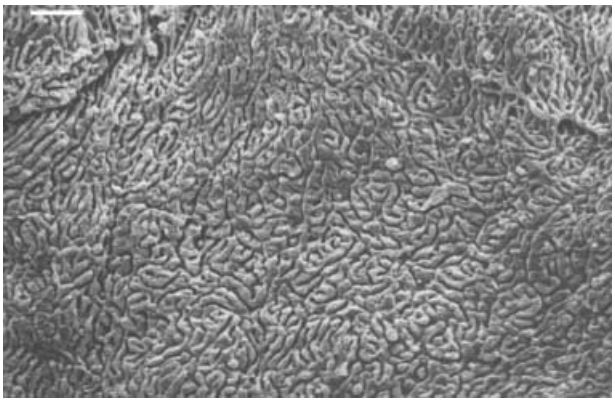

Fig. 11 Very pronounced microfolds situated in the bare region. 5000x. Bar, 2 μm.

(1988) and Yoshimura et al. (2002), we believe that, because of their size and morphology, they possess characteristics which make them worthy of being considered a separate group. In other species of carnivorans conical papillae have a smooth surface and are not very prominent (Chamorro et al. 1987; Iwasaki et al. 1987a; Emura et al. 2000c), whilst those encountered in the giant panda are longer, flattened, are directed posteriorly and have on their borders secondary projections like the teeth of a saw. The size, morphology and position of these papillae are similar to those described by Yoshimura et al. (2002) in the sea lion (*Zalophus californianus californianus*). The mucus-secreting pores and the microfolds distributed on the papillary surfaces resemble those of other carnivorans. As in other mammals, these papillae probably have a mechanical function, although their size and degree of keratinization are less than the filiform papillae.

Filiform papillae

As is the case among all mammals, these are the most numerous mechanical papillae on the tongue and are distributed along the entire surface of the lingual dorsum as well as on the ventral surface close to the tip, as described by Davis (1964). The different morphologies of these papillae correspond to those described in other mammals. Those with multiple filaments present secondary papillae on their surface such as those found in the dog (*Canis familiaris*) (Kobayashi et al. 1988) and the silver fox (*Vulpes vulpes fulva*) (Jackowiak & Godynicki, 2004). Given their dimensions and position, their function is likely to be purely mechanical, increasing the friction produced by the tongue during grooming and rasping food. At a high degree of magnification the folds and pores are like those of other mammals. Owing to their size and smaller number, the multi-filamentous papillae on the inferior surface might fulfil a mechanical cleaning function in the inter-dental spaces of the lower jaw, as occurs in other mammals such as prosimians and tupaias (Hofer et al. 1993). The filiform papillae in the form of a crown resemble those of the cat (Chamorro et al. 1987), the Japanese black bear (Inatomi & Kobayashi, 1999), the tiger (Emura et al. 2004) and other carnivorans (Kobayashi & Wanichanon, 1992).

Fungiform papillae

These are in all ways similar to those found in other mammals, rounded and encircled by filiform papillae which give the appearance of protecting them. Their gustatory function is clear in view of their possessing multiple taste pores on their surface. As is the case with other carnivorans, they tend to be located in the anterior two thirds of the tongue.

Vallate papillae

In other mammals these papillae may have two principal morphologies: simple or compound. The simple type has a not-very-prominent uniform central part, surrounded by a deep groove, whilst the compound papillae have a central part divided by secondary grooves. The number of secondary papillae is quite variable even within the same species (from 13 to 42 in our specimen). Occasionally double or triple papillae are present which share a primary groove. In the panda the papillae are compound, as in Perissodactyla (Chamorro et al. 1986; Emura et al. 2000a), certain artiodactyls (Chamorro et al. 1986; Emura et al. 1999) and in carnivorans such as the cat (Chamorro et al. 1987), Asian black bear (Inatomi et al. 1999; Emura et al. 2001), silver fox (Jackowiak et al. 2004) and sea lion (Yoshimura et al. 2002).

Like Davis (1964), we did not find any foliate papillae. In contrast, Raven (1936) identified two symmetrical clefts on the lateral borders of the tongue as foliate papillae. The gustatory and secretory pores, together with the microfolds, are similar to those described in other mammals and, sharing the view of Iwasaki et al. (1987b), we believe that their morphology results from the evolution of keratinized papillary surfaces as an adaptation to diet and bolus formation.

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We consider the bare region of the tongue's surface to be the result of repeated friction from hard food; in fact, the microfolds in this region are more complex (Fig. 11) than in others. The smooth patch may be interpreted as a consequence of the repeated friction of the bamboo shoots, as the bamboo is taken and cleaned by lateral insertion in the mouth, behind the canines, followed by transverse sliding between the tongue, teeth and palate.

In all, the morphology of the lingual papillae of the giant panda has characteristics of both herbivores and carnivores. The distribution, structure and morphology of the papillae are basically those of a carnivoran, although adaptation to a herbivorous diet has caused the filiform papillae to have very prominent pseudo-papillae with a mechanical function and one of protecting the fungiform papillae. The number of vallate papillae is more similar to that of carnivorans than to herbivorous species. The presence of secondary papillae in the vallate papillae is uninformative, as they appear in several groups of mammals with no obvious relationship to diet.

The apparent adaptation of the giant panda (a carnivoran) to a herbivorous diet may not yet be complete, with a mix of elements on the lingual surface.

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References

Barone R (1976) *Anatomie comparée des mamifères domestiques. Tome troisième, Splanchnologie, Laboratoire d'Anatomie*. Lyon: Ecole National Vetérinaire.

Chamorro CA, De Paz P, Sandoval J, Fernández JG (1986) Comparative scanning electrón-microscopic study of the lingual papillae in two species of domestic mammals (*Equus caballus* and *Bos taurus*). I. Gustatory papillae. *Acta Anat* **125**, 83–87.

Chamorro CA, Sandoval J, Fernández JG, Fernández M, y de Paz P (1987) Estudio comparado de las papilas linguales del gato (*Felis catus*) y del conejo (*Oryctolagus cuniculus*) mediante el microscopio electrónico de barrido. *Anat Histol Embryol* **16**, 37–47.

David A (1869) Etrait d'une lettre du même, dateé de la Principaute Thibetaine (independente) de Mou-pin, le 21 Mars 1869. *Nouv Arch Mus Hist Nat Paris, Bull* **5**, 12–13.

Davis DD (1964) The giant panda: a morphological study of evolutionary mechanism. *Fieldiana Zoolology Memoirs* **3**, 1–339.

De Paz P, Chamorro CA, Sandoval J, Fernández M (1988) Comparative scanning electron-microscopic study of the lingual papillae in two species of domestic mammals (*Equus caballus* and *Bos taurus*). II. Mechanical papillae. *Acta Anat* **132**, 120–123.

Dierenfeld ES, Hintz HF, Robertson JB, Van Soest PJ, Oftedal OT (1982) Utilisation of bamboo by the giant panda. *J Nutr* **112**, 636–641.

Eichelberger MA, Wildt DE, Bush M (1985) Constructing a molecular phylogeny of the giant panda (*Ailuropoda melanoleuca*). *Bongo (Berlin)* **10**, 175–182.

Emura S, Tamada A, Hayakawa D, Chen H, Yano R, Shoumura S (1999) Morphology of the dorsal lingual papillae in the blackbuck, *Antilope cervicapra*. *Okajimas Folia Anat Jpn* **76**, 247–253.

Emura S, Tamada A, Hayakawa D, Chen H, Shoumura S (2000a) Morphology of the dorsal lingual papillae in the black rhinoceros (*Diceros bicornis*). *Anat Histol Embryol* **29**(6), 371–374.

Emura S, Tamada A, Hayakawa D, Chen H, Shoumura S (2000b) Morphology of the dorsal lingual papillae in the barbary sheep, *Ammotragus lervia. Okajimas Folia Anat Jpn* **77**, 39–45.

Emura S, Tamada A, Hayakawa D, Chen H, Shoumura S (2000c) Morphology of the dorsal lingual papillae in the bush dog (*Spheothos venaticus*). *Okajimas Folia Anat Jpn* **77**(5), 137–141.

Emura S, Hayakawa D, Chen H, Shoumura S (2001) Morphology of the dorsal lingual papillae in the newborn panther and Asian black bear. *Okajimas Folia Anat Jpn* **78**(5), 173–177.

Emura S, Hayakawa D, Chen H, Shoumura S (2004) Morphology of the lingual papillae in the tiger. *Okajimas Folia Anat Jpn* **81**, 39–44.

Evan AP, Dail WG, Dammrose D, Palmer C (1976) Scanning electron microscopy of cell surfaces following removal of extracellular material. *Anat Rec* **185**, 433–447.

Goldman DP, Giri R, O'Brien SJ (1989) Molecular genetic-distance estimates among the Ursidae as indicated by one- and two-dimensional protein electrophoresis. *Evolution* **43**, 282–295.

Hofer HO, Castenholz A, Zöltzer H (1993) The sublingua and tongue of tupaia (Scandentia, Mammalia): a scanning electron microscope study. *Folia Primatol* **60**, 185–194.

Inatomi M, Kobayashi K (1999) Comparative morphological studies on the tongue and lingual papillae of the Japanese black bear (*Carnivora*) and the mountain goat (*Artiodactyla*). *Shigaku* **87**, 313–328.

Iwasaki S (2002) Evolution of the structure and function of the vertebrate tongue. *J Anat* **201**, 1–13.

Iwasaki S, Miyata K, Kobayashi K (1987a) Comparative studies of the dorsal surface of the tongue in three mammalian species by scanning electron microscopy. *Acta anat* **128**, 140–146.

Iwasaki S, Miyata K, Kobayashi K (1987b) The surface structure of the dorsal epithelium of tongue in the mouse. *Acta Anat Nippon* **62**(2), 69–76.

Jackowiak H, Godynicki S (2004) The scanning electron microscopic study of lingual papillae in the silver fox. *Ann Anat* **186**, 179–183.

Kobayashi K, Miyata K, Takahashi K, Iwasaki S (1988) Developmental and morphological changes in dog lingual papillae and their connective tissue papillae. In: *Regeneration and Development, Proceedings of the 6th International M. Singer Symposium, Maebashi, Japan*, pp. 609–618.

Kobayashi K, Wanichanon C (1992) Comparative studies on the stereo architecture of the lingual connective tissue cores in the tree shrew. *Anat Embryol (Berl)* **186**, 511–518.

Mayer FSC (1844) Über die Zunge als Geschmacksorgan. *Nova Acta Acad Leop-Carol Nat Cur T* **20**, 721–748.

Münch F (1896) Die Topographie der Papillen der Zunge des Menschen und der Säugetiere. *Morph Arb* **6**, 605–684.

O'Brien SJ, Nash WG, Wildt DE, Bush ME, Benveniste RE (1985) A molecular solution to the riddle of the giant panda's phylogeny. *Nature* **317**, 140–144.

Raven HC (1936) Notes on the anatomy of the viscera of the giant

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panda (*Ailuropoda melanoleuca*). *American Museum Novitates* **877**, 1–23.

Scala G, Pelagalli GV, Vittoria A, Girolamo P (1993) Etude Morpho-structurale des papilles linguales chez le buffle (*Bubalus bubalis*). *Anat Histol Embryol* **22**, 264–272.

Shimoda T, Nakanishi E, Yoshino S, Kobayashi S (1996) Light and scanning electron microscopic study on the lingual papillae in the newborn sea otter, *Enhydra lutris. Okajimas Folia Anat Jpn* **73**, 65–74.

Sicher H (1944) Masticatory apparatus in the giant panda and the bears. *Field Mus Nat Hist Zool Ser* **29**, 61–73.

Sonntag CF (1920) The comparative anatomy of the tongues of the mammalia. I. General description of the tongue. *Proc Zool Soc Lond* **IX**, 115–129.

Sonntag CF (1923) The comparative anatomy of the tongues of the mammalia. VIII. Carnivora. *Proc Zool Soc Lond* **IX**, 129–152.

Stadtmüller F (1938) *Handbuch der Vergleichenden Anatomie der Wirbeltiere*. Berlin-Wien.

Thenius E (1979) Zur systematischen und phylogenetischen Stellung des Bambusbären: *Ailuropoda melanoleuca* David (Carnivora, Mammalia). *Z Saugatierkd* **44**, 286–305.

Waits LP, Sullivan J, O'Brien SJ, Ward RH (1999) Rapid radiation events in the family Ursidae indicated by likelihood phylogenetic estimation from multiple fragments of mtDNA. *Mol Phylogenet Evol* **13**, 82–92.

Wilson DE, Reeder DM (1993) *Mammal Species of the World. A Taxonomic and Geographic Reference*, 2nd edn. Washington: Smithsonian Institution press.

Yoshimura K, Shindoh J, Kobayashi K (2002) Scanning electron microscopy study of the tongue and lingual papillae of the California sea lion (*Zalophus californianus californianus*). *Anat Rec* **267**, 146–153.

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